INHERITANCE IN AN OAK SPECIES HYBRID

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With eight text figures

A report of the first generation of the cross *Quercus virginiana* (Live Oak) × *Q. lyrata* (Overcup Oak)[1] was made by the late Helge Ness (1918) who, a few years later, was successful in obtaining three second generation families totaling twenty-three plants. While Professor Ness raised this second generation to fruiting maturity, he never made a second report. This paper presents a study of segregation of characters in the above F_2.

The original cross was made in 1909 using the Live Oak as female; this was duplicated the following year. This species cross is easily made in spite of the fact that the parents belong to extremes of the section Lepidobalanus. Two of the four F_1 trees planted in front of the Station buildings are still growing vigorously and correspond very closely to the early description. They show definite evidence of hybrid vigor. They are now 13.4 and 14.8 inches in diameter at four and one-half feet above the ground. Eleven Live Oaks planted three years later average only 5.8 inches in diameter at the same height. Twenty Overcup Oaks planted with the Live Oaks average 5.97 inches. While the F_1 hybrids are perhaps a little more advantageously situated than the others, their diameter, which is more than twice that of plants of either parental species, can not be accounted for either by their situation or by their three-year start. All F_1 plants of this cross were especially vigorous growers as seedlings.

The 23 second generation hybrids belong to three families as follows: five trees from F_1 parent No. 1, ten from parent No. 2 and nine plants from parent No. 5. F_1 parent No. 1 resulted from the 1909 cross; parents No. 2 and No. 5 from the later cross. Since the F_1 plants are quite uniform and since the numbers in the second generation are small, all F_2 plants have been considered together as a single family. Seed to produce the second generation was collected in 1919, the trees being set out in 1923, spaced ten feet apart each way.

[1]It is an interesting fact that trees supposed to be natural hybrids between the Live Oak (*Quercus virginiana*) and the Overcup Oak have been found in several places along the Gulf coast. Specimens from a number of trees found in the vicinity of Natchez, Mississippi, by Miss C. C. Compton were sent to the Arnold Arboretum in 1915 and 1916, and Professor Sargent published a description of them under the name *Quercus Comptonae* in the Botanical Gazette, LXV. 456-458 (1918).

The earliest discovery of the tree, however, seems to have been by Dr. Chas. H.

LEAF CHARACTERS

The leaves of the Overcup Oak are approximately twice as long as those of the Live Oak. While the leaves of the F_1 plants are large, they are smaller than those of the male parent. A random sample of 50 mature leaves were secured from each second generation tree and from representatives of the parental species. Measurements were taken, in centimeters, of the length and greatest width. The means of these two dimensions were added to serve as an arbitrary index of leaf-size. In relation to leaf-area this method exaggerates the size of the *lyrata*-type leaf. The results are presented in Figure 1. The F_2 plants fall into

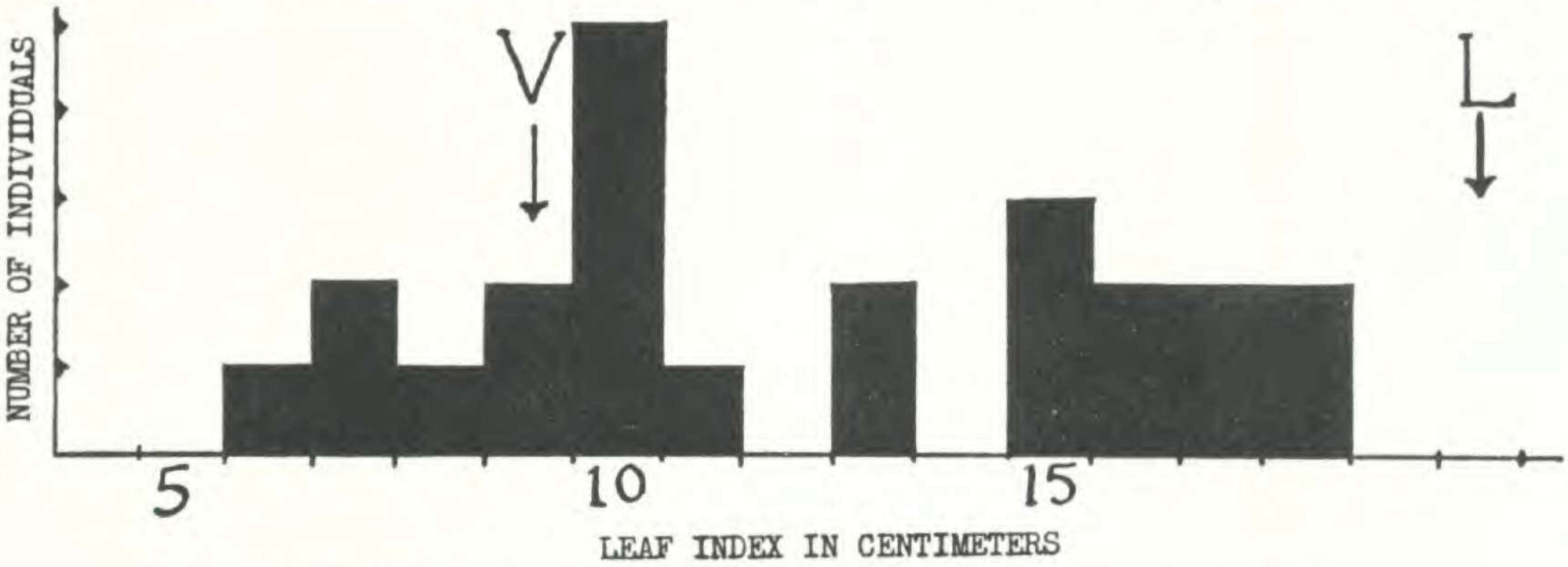

FIGURE 1. SEGREGATION OF LEAF SIZE IN THE F_2.
The indices of the parental species are marked by arrows.

two distinct groups, one ranging around the *virginiana* parent, the other in a distribution below the *lyrata* parent. The curve of the first group shows a decided tendency to flatten out, the other group forms approximately a straight line. The two groups are about equal in size, there being 12 individuals in the first and 11 in the second. This occurrence

Mohr, along Paysons Creek, Matagorda Co., Texas. A specimen of his collection, No. 96, Dec. 18, 1880, is now in the herbarium of the Arnold Arboretum. The label on this specimen also bears the notation: "A large low wide-spreading tree, with persistent foliage." The foliage is of the "small-leaf" group of Dr. Yarnell. The tree seems to have disappeared from this locality, or at least a diligent search for it by the writer in 1916 failed to find any trace of it.

It is not stated on Dr. Mohr's label whether the tree found by him was native or planted, but in the absence of such notation, it may be assumed that it was wild. With the exception of this and of two seedlings found in the woods near Natchez, all of the trees known seem to have been planted either in parks, as street trees, or about dwellings and plantations. But no records were obtained as to where they came from, except in the case of some trees in New Orleans, which were reported to have been brought from across Lake Pontchartrain 30 or 40 years previously.

Miss Compton, as stated by Sargent, located some 20 or 30 trees of this hybrid growing in the vicinity of Natchez, and specimens in the herbarium here show it to have been collected near Selma, Alabama, and along the streets and in Audubon Park, New Orleans. These specimens show a wide variation in leaf and fruit characters, with many of them intermediate between the two parents, and similar to those described by Dr. Yarnell for the Ness hybrid and its descendants.

The rather wide natural distribution would seem to indicate that the two species, in spite of their obvious morphological differences, hybridize readily when growing together.

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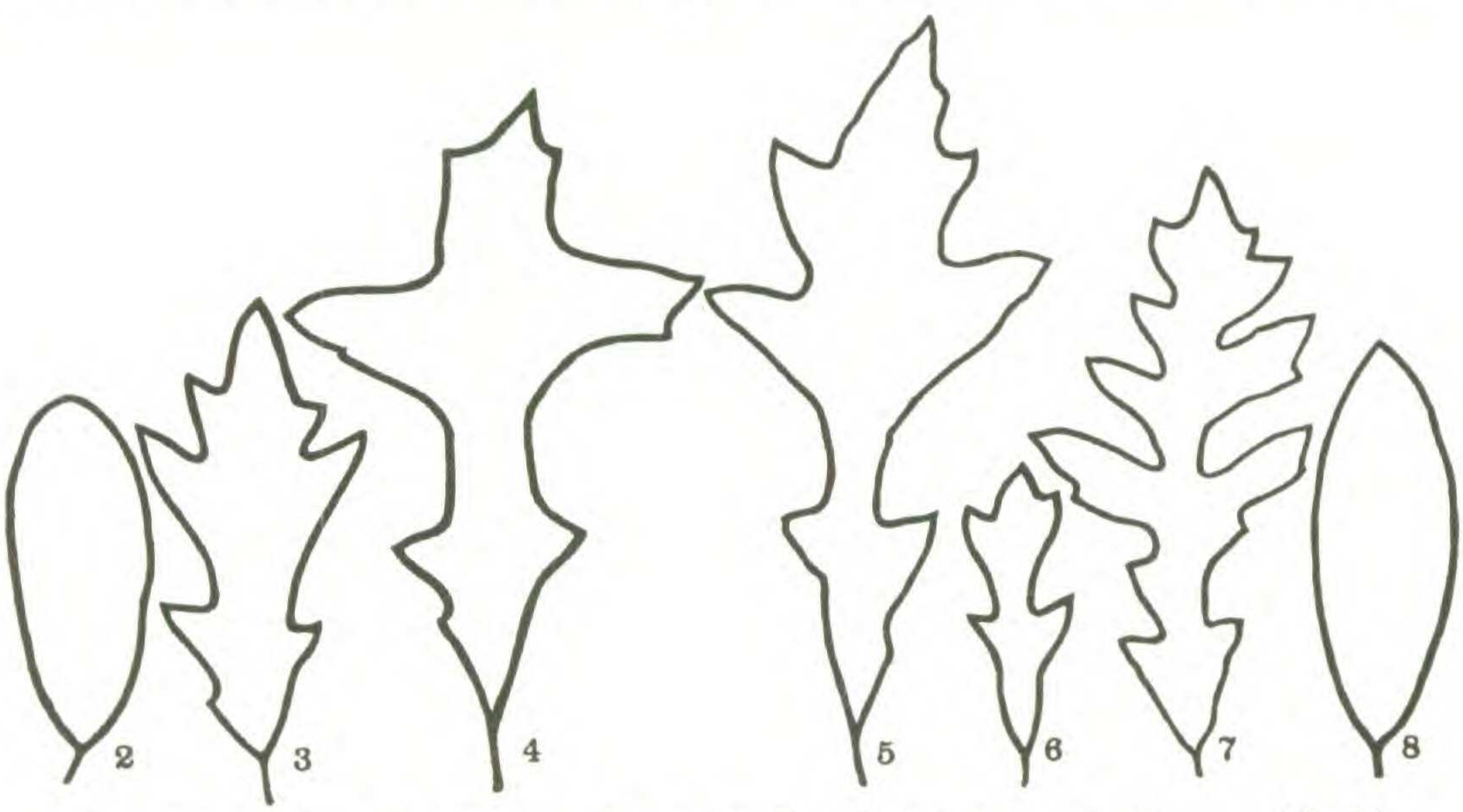
of two distinct groups of approximately equal size has been interpreted as evidence that two principal factors are involved in size of leaf and that the distribution obtained represents a 9:7 ratio, the lack of agreement being due to small numbers.

Since segregation is taking place in the second generation of a rather wide interspecific cross, it is reasonable to assume that a number of factors from one species influence the expression of characters normally found in the other. Such an influence is evident in the expression of each of the characters under study, but does not, it is believed, invalidate an estimate of the number of principal factors involved. This, together with a lack of complete dominance, accounts for the amount of variation found in the second generation.



FIGURES 2–8. PARENTAL, F_1 AND F_2, LEAF SHAPE TYPES, × ¾. 2. QUERCUS VIRGINIANA. 3. THE F_1. 4. Q. LYRATA. 5–8. F_2 PLANTS.

Perhaps the most difficult classification to make, on this account, is that of leaf shape. The male parental species derives its name from the lyrate character of its foliage. The leaf of the female parent, while for the most part entire, does show a tendency toward the production of slight irregularities on some of the leaves, producing a type of margin which can not be distinguished, except in degree, from certain of the F_2 segregates. The *virginiana* type may be seen in Figure 2, the *lyrata* type in Figure 4. The F_1 is outlined in Figure 3. The figures have been traced from representative leaves and have been reduced ¼ in reproduction. Figures 5 and 8 illustrate extreme types in the F_2. The leaf in Figure 5 is the closest approach to the *lyrata* type. The leaf in Figure 8 is *virginiana*-like except for the apex which is pointed. There is one such plant. Three others have leaves very close to those of the female parent, with the addition of small lobes. Seven others are considered nearer this type. All of these are in the "small-leaf" group discussed above. The leaf in Figure 6 illustrates the only plant in the "small-leaf" group which is distinctly lyrate in shape. All trees in the "large-leaf" group have lyrate leaves. The exact form in some cases varies rather widely from the *lyrata* type as may be seen in Figure 7. This is presumably due to this influence of incidental factors from the Live Oak parent. The fact that one recessive was recovered in the F_2 and that all such plants can be placed in two general categories is good evidence that not more than two principal factors are involved in determining leaf shape. Since the grouping with respect to size and shape of leaves coincide with one exception, the relationship of the two groups of factors can not be determined. A number of things might be responsible, such as identity or close linkage of factors, gametic selection, or inviability of certain gametic or zygotic combinations.

The epidermis of the Live Oak is somewhat thickened, giving the leaves a shiny appearance, in contrast to the duller and thinner leaves of the Overcup Oak. The coriaceous character is not completely dominant in the F_1, heterozygous plants being classified as modified coriaceous. The leaves of all plants in the "small-leaf" group were coriaceous. In addition, the leaves of three trees in the "large-leaf" group were given the same classification. This gives a total of 15 coriaceous and 8 non-coriaceous plants. This is a little nearer the 9:7 than to the 3:1 expectancy (13:10 and 17.25:5.75 respectively).

A related character is the habit of dropping or retaining the leaves at the end of the summer season. The name "Live Oak" is due to the evergreen character of *Q. virginiana.* The pollen parent, on the other hand, sheds its leaves relatively early. The first generation hybrid holds only a part of its leaves during the winter. All of the trees with large, non-coriaceous leaves are completely deciduous. In addition, two of the three trees with large modified coriaceous leaves were fully deciduous, while the third was classified as deciduous with a tendency to hold a part of its leaves later in the season. Five of the twelve trees with "small" coriaceous leaves were completely evergreen, the remainder being partially evergreen. It is evident that not more than two principal factors are involved here and quite possibly only one pair.

FRUIT CHARACTERS

Fruits of the two parental species differ widely in appearance, especially in regard to size, shape and character of the cupule. Twelve of the twenty-three second generation trees fruited during the 1931 season.

Fruits of *Q. virginiana* are approximately twice their diameter in length while those of *Q. lyrata* are somewhat wider than long. In the F_1 the fruits are wider in proportion to length than those of the female parent. Acorns of eight trees are distinctly long, of two are intermediate, and of two decidedly round, giving a total of 8 long to 4 round. Inheritance of fruit shape seems to be similar to that of leaf shape with the former giving more nearly complete dominance. The fact that no fruits precisely like those of the *lyrata* parent have been found lends support to a two-factor hypothesis.

There is a striking difference between the two species in size of fruit, the larger diameter of *lyrata* fruit giving the greater volume. Acorns of the first generation usually exceed those of either parent in size since they are somewhat longer than those of *virginiana* and nearly as wide as in *lyrata*. In every case in the F_2 the fruits have been classified as small and in three individuals the fruit is considerably smaller than in the *virginiana* parent. How much of this may be due to irregularities of development resulting from the interspecific nature of the cross can not be said. It is clear that the results can not be explained on a simple factorial basis.

The Overcup Oak is so named because the cupule covers from three-fourths to nearly the entire nut. In the Live Oak fully three-fourths of the acorn is exposed. The cupule of the first generation is intermediate in size, covering from one-third to one-half of the large acorn. In nine F_2 plants the cupule is about as found in the female parent. In two trees the cupule is intermediate in size, and in one the cupule approaches but does not equal that of the pollen parent in size. While two factors are indicated in this case it is evident that the results are complicated by other factors such as size of fruit.

Thickness of cupule scales is a related character. While the scales are nearly equal in number in the two species they are much enlarged in the Overcup Oak and have a protuberance at the tip. The cupule scales in the F_1 may be said to be intermediate in size, although they are much closer to those of the Live Oak parent. In the F_2 eight individuals have thin scales and five have scales intermediate in thickness. None has scales approaching those of the Overcup Oak in prominence. Since this character shows such a close relationship with the preceding it is likely that the two have one factor in common.

BARK CHARACTER

It has been possible to obtain data in regard to one other character, type of bark. In *Q. lyrata* the bark flakes off, while in *Q. virginiana* the bark of the trunk is rough. The first generation trees are intermediate in this respect. In the second generation 7 trees have bark exhibiting different degrees of flakiness while 16 trees have a rough trunk. This ratio is probably the result of segregation of a single factor pair. This character, in common with the others under consideration, exhibits considerable variability in the F_2.

DISCUSSION

Augustine Henry (1910) studied large numbers of seedlings (971) of what was very likely the second generation of a natural cross between *Ulmus foliacea* and *U. glabra*. The F_1 had received the name *U. vegeta,* known popularly as the Huntingdon Elm. Seedlings of both parental species were quite uniform. Three characters, opposite vs. alternate leaves, leaf size, and length of petiole, were found to segregate on a 3:1 basis in the second generation. Different F_2 trees were found to vary greatly in degree of fertility.

Plate 24 of the paper cited above illustrates the Lucombe Oak, parents and seedlings. The leaf size and shape combinations in the F_2 are very similar to those of the Live × Overcup Oak cross. The Lucombe is evidently a seedling of a *Q. cerris* (Turkey Oak) × *Q. suber* (Cork Oak) cross. It is subevergreen and was propagated by grafting at Exeter, England in 1763. In 1792 acorns of this Oak were sown which gave a variable progeny (Henry 1910). The author recognizes hybrid vigor in the first generation of these and other tree crosses and the resulting increase in usefulness, and later made numerous controlled crosses with this end in view.

H. A. Allard (1932) has made a study of a number of natural Oak hybrids growing in or near the District of Columbia. Open pollinated seed of *Q. Saulii,* considered to be a hybrid between *Q. alba* and *Q. montana,* were planted about 1922. Forty seedlings grew, most of which survived. Characters of *Q. montana* are more evident in the "F_2" than those of *Q. alba*. The author points out that the generation involved is necessarily unknown. No factorial analysis was attempted. He reports that D. T. McDougal (1907) raised 55 seedlings of Bartram's Oak (*Q. heterophylla*), a natural hybrid between *Q. phellos* and *Q. borealis maxima*. Plants similar to each parent and various types of intermediates were obtained.

The first generation of the Live and Overcup Oak cross shares with other interspecific tree crosses the characteristic of rapid growth. In habit of growth it is intermediate between its two parents, being more erect than the Live Oak and having a greater spread than the Overcup parent. As a result, it is much more attractive as an ornamental than the latter species. Growth of the second generation trees varies widely, from somewhat better than the parental species to individuals that are decidedly stunted.

The tendency for characters of one parent to be inherited together in the F_2 is striking. It is a problem of importance to the plant breeder who makes use of interspecific crosses. Normal chromosomal linkage would account in some measure for this result, especially since it is likely that there is less crossing over in the F_1 than in either pure species. The partial sterility found in the second generation is good evidence that the chromosomal complements of the two species are sufficiently differentiated to prevent their normal functioning in certain combinations. It is but a step to assume that other combinations are unable to produce a viable individual. The chance for securing the desired grouping of characters under such conditions will depend upon the size of F_2 or back cross populations, which present an opportunity for viable chromosome combinations carrying the desired characters.

The results suggest, for example, that the evergreen character might be combined with hardiness to extend the range of the Live Oak type considerably north of Virginia. This would involve a number of genes from each species such as those for thickened epidermis, leaf-size, and also for physiological characters. Such a successful combination, while not common in the F_2 would be expected to occur frequently enough to justify a systematic search for such individuals.

There is ample evidence that the normal expression of a character is frequently modified by new combinations of genes from the two species. The idea that a gene may influence the expression of characters which are determined primarily by other genes has been frequently advanced. This idea usually carries with it the assumption that either allelomorph has the same incidental effect regardless of differences in the morphological expression of the allelomorphic pair. The fertile species cross with its high variability of character expression in the second generation bears out the above assumptions, in that what are presumably allelomorphic genes in the two species seem to have different incidental effects in contrast to the situation for an allelomorphic pair within a single species.

The low number of principal factors involved for many characters increases the chance of securing a satisfactory combination in the second generation. Inheritance in forest trees thus appears to be no more complex than inheritance in most material of interest to the plant breeder.

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